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Post-1900 Mule Deer Irruptions In The Intermountain West:

#b Principle Cause and Influences

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RESEARCH SUMMARY

This report evaluates four hypotheses for the dramatic increase in mule deer populations that occurred in the Intermountain West between the early 1930's and mid-1960's:

1. Succession of rangelands from grass dominance to dominance by woody plants created vast expanses of optimum mule deer habitat.
2. Conversion of coniferous forests to shrubfields by logging and wildfire improved mule deer habitat, especially the availability of browse.
3. Conservation and predator control dramatically reduced deer mortality.
4. Reductions in numbers of livestock on the open range increased the amount of forage available to mule deer.

The author's investigations of mule deer populations, mule deer ecology, and long-term trends in plant communities support hypothesis 1—succession of grasses to woody plants was the principal cause of the mule deer irruptions; the remaining hypothetical factors contributed but were not critical. The invasion of woody plants was set in motion by intensive grazing, which suppressed or eliminated competing grasses, and by a marked reduction in the size, intensity, and frequency of fires, which had periodically eliminated and suppressed woody plants, and had maintained ranges that were predominantly bunch-grasses. The absence of fire was brought about by the reduction in potential fuels by intensive grazing, elimination of Indian ignitions, breakup of fuel continuity by development of ranches, communities, and roads, and organized fire suppression.

Conversion of forests to shrubfields by logging and wildfire affected a relatively small part of the West, hence had localized impact on deer numbers. Similarly, conservation and predator control, and reductions in livestock numbers, alone could not have been more than contributing factors.

Mule deer habitats reached the optimum balance of trees, shrubs, and herbs during and following a period of extreme disturbance by livestock grazing and absence of fire on the open range, and fire and logging in the forests. In recent decades this habitat has deteriorated as succession proceeds toward overly large, dense stands of shrubs and trees that are not as productive as in former years. The productivity of mule deer habitats in the Intermountain West can only be restored and maintained by reintroducing or simulating the perturbations that created them: judicious use of grazing, logging, and prescribed fire.

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Post-1900 Mule Deer Irruptions in the Intermountain West: Principal Cause and Influences

George E. Gruell

INTRODUCTION

Between the early 1930's and the mid-1960's, mule deer (*Odocoileus hemionus*) populations irrupted in the Intermountain West: the States of Montana, Wyoming, Idaho, Utah, and Nevada. Speculation about the causes of the irruption can be hypothesized as follows:

1. Succession of rangelands from dominance by grasses to dominance by woody plants that constitute superior mule deer habitat (Julander 1962; Leopold 1950; Longhurst and others 1976).
2. Conversion of forests to shrubfields by wildfire and logging, which generally resulted in improved deer habitat, particularly availability of browse (Lyon 1969; Pengelly 1963).
3. Conservation and predator control dramatically reduced deer mortality (Leopold and others 1947; Rasmussen and Gaufin 1949).
4. Reduction in numbers of livestock on the open range increased the amount of forage available to mule deer (Rasmussen and Gaufin 1949; Salwasser 1976).

The author's observations of mule deer populations and his studies of plant communities in the Intermountain West support hypothesis 1—that succession from grass dominance to trees and shrubs that comprise optimum mule deer habitat was indeed the principal reason for the explosive increase in mule deer numbers after 1930, to which the other factors contributed.

Although various authors have speculated on the causes of succession toward woody plants—commonly attributed to disruption of grasses by intensive grazing or absence of fire—none has treated these factors in great depth. The principal contribution of this report is to provide additional insight into how this vast transformation in plant communities came about, particularly the role of fire prior to and after settlement of the Intermountain West. A discussion of the fire ecology of western rangelands, with emphasis on the implications for mule deer habitat, constitutes most of the dissertation on hypothesis 1.

An ancillary goal of this report is to forge an environmental perspective that will provide a more effective basis for managing mule deer populations, which heretofore has been mainly regulating the size of the harvests. Mule deer habitats reached optimum condition earlier in the century in response to various perturbations—intensive grazing and fire suppression on the open ranges, wildfire and logging in the forests. In recent years, this habitat has declined in quality, mainly

because of the absence of fire, and it will continue to decline unless periodically rejuvenated by judicious grazing, logging, and prescribed burning.

Marked reductions in mule deer populations following the mid-1960's (Julander and Low 1976) are not addressed in this paper. In retrospect it appears that this phenomenon was the result of several interrelated factors including a deterioration in habitat quality, marked decline in fawn production, and sustained high hunter harvest that reduced the breeding population and increased effectiveness of predation on a reduced deer population.

HYPOTHESIS 1: SUCCESSION FROM GRASS DOMINANCE TO DOMINANCE BY WOODY PLANTS

Most of the support for hypothesis 1 is devoted to an analysis and description of the plant communities of the Intermountain West prior to settlement, their succession from grasses to woody plants, and the agents that set succession in motion. Because fire had such a profound influence on this phenomenon, this section includes an extensive dissertation on the fire history and fire ecology of Intermountain rangelands and forests. To enable the reader to evaluate important relationships between the transformation of the plant communities and the deer irruption, particularly timing, geographic scope, relative numbers of animals, and the implications of succession on deer habitat, the section on plant communities is preceded by brief reviews of the deer irruption and mule deer ecology. Much of the evidence presented in support of hypothesis 1 is also germane to discussions of hypotheses 2, 3, and 4.

Mule Deer Populations

It is commonly believed that mule deer were relatively few in the Intermountain West prior to and during the early stages of Euroamerican settlement (Julander and Low 1976; Leopold and others 1947; Leopold 1950). These conclusions, however, were largely based on records from Utah and California. A review of written accounts covering Montana, Wyoming, Idaho, Utah, and Nevada (appendix 1) suggests that there were regional differences in early mule deer population levels.

Mule deer were apparently common or even plentiful in some localities in Montana, Wyoming, and perhaps central Idaho, whereas in other localities they were

uncommon or scarce. An exaggerated idea of mule deer numbers may have been formed, however, in instances where the observer did not distinguish between mule deer and whitetailed deer (*Odocoileus virginianus*). "Deer" reported in bottomland habitats were probably whitetailed deer, not mule deer. An exaggeration of mule deer numbers may also derive from reports of winter concentrations comprised of animals from low-density summer ranges.

The early record suggests scarcity of mule deer in Utah, Nevada, and southern Idaho. Only two accounts were found that described the presence of deer, and these were localized winter concentrations. Reports from northern Nevada during Hudson Bay Company expeditions from 1826 to 1831 are particularly noteworthy because they make no mention of deer despite numerous hunting excursions in mountain ranges that later supported great numbers of mule deer.

Leopold (1950) suggests that, before Euroamerican settlement, mule deer were found principally where forest and grasslands met, or on recent burns. Pengelly (1963) reports that most early accounts in northern Idaho referred to the abundance of deer (including mule deer) on the forest edge. Both authors emphasized seral vegetation in forests as being essential to production of deer.

During the mining and homesteading era (1847 to 1900), mule deer were subjected to extreme exploitation. By 1900, numbers had been seriously depleted in Utah (Rasmussen and Gauvin 1949). Julander and Low (1976) report similar conditions in other western States. In 1917, for example, the deer population in Nevada's 600-mi² Ruby Mountains was reported to number about 50 animals (1917 Annual Wildlife Reports, Humboldt National Forest files [USDA Forest Service 1917]). Borell and Ellis (1934) concluded from a 1927 survey in the Ruby Mountains that the low deer population reflected marginal habitat, and that this mountain range would never support large numbers of deer.

My conversations with longtime Nevada residents during the mid-1950's revealed that sighting a deer was a novelty until the 1930's, and tracks were a subject worthy of discussion. Julander and Low (1976) tell of an oldtimer in Utah who recalled as a youth (around 1900) following the tracks of a deer 4 consecutive days before getting a fleeting glimpse of the animal. Similar accounts have been given by early residents of Montana (Bayless 1975). For example, Koch (1941) reported that the sighting of a single deer, elk, or sheep during the 1890's was most unusual.

Mule deer populations began increasing regionally in the 1930's. In Wyoming, Murie (1951) reported that mule deer in the Jackson Hole region were scarce prior to 1930, but increased remarkably by 1950. By the mid-1950's the Nevada Fish and Game Department estimated that the Ruby Mountains population numbered between 25,000 and 30,000 animals. In Utah the mule deer population was estimated to have increased from 8,500 in 1916 to a peak of 375,000 in the 1945-50 period. Idaho officials estimated that their deer population (including whitetailed deer) increased from 45,000 in 1923-24 to 315,000 in 1963 (Julander and Low 1975).

Mule Deer Habitat Preferences

Most authorities agree that mule deer are primarily browsers and, therefore, benefit from increases in shrubs. Various research supports this assumption (Kufeld and others 1973; McAdoo and Klebenow 1979). Shrubs are particularly important during winter months (Hill 1956). Key plants in a north-central Utah study were big sagebrush (*Artemisia* spp.) and mountain-mahogany (*Cercocarpus* spp.) (Richens 1967). In the Bridger Mountains of Montana, Wilkins (1957) concluded that big sagebrush, bitterbrush (*Purshia tridentata*), and Rocky Mountain juniper (*Juniperus scopulorum*) constituted the major items in the diet of wintering deer. In the Missouri River Breaks, big sagebrush was the single most important browse plant (Mackie 1970). Big sagebrush was also the most important food consumed over the critical winter months in the Lassen-Washoe and Inyo Ranges in California and Nevada (Leach 1956). When viewed in the context of yearlong diets, forbs often comprise a large portion of forage intake on summer ranges (Kufeld and others 1973; Lovaas 1958; Wilkins 1957). Green grass usually comprises most of the diet during a short period of initial spring growth.

Various studies have demonstrated that snow depth and duration on winter range are a major determinant of mule deer population levels (Edwards 1956; Picton and Knight 1969; Robinette and others 1952; Wallmo and Gill 1971). Most mule deer winter ranges are snow covered at least part of the winter. Thus, it appears that conversion of ranges from herb dominance to shrub dominance improved forage availability and nutritional quality, particularly during stress periods when all but the taller forage species were snow covered. Winter survival of deer proved to be better on these shrub-dominated ranges (Harper 1968).

The importance of cover, including favorable terrain, has also been widely recognized. During severe weather deer abandon good food supplies in favor of protection (Loveless 1967). The clearing of pinyon-juniper woodland in New Mexico improved food quality, but the absence of cover apparently reduced habitat quality enough to limit use by deer (Short and others 1977). Expansion of pinyon-juniper into grasslands and shrublands increased the capacity of these ranges to support wintering mule deer up to the point where trees began displacing forage plants. Expansion of Douglas-fir (*Pseudotsuga menziesii*), limber pine (*Pinus flexilis*), and ponderosa pine (*Pinus ponderosa*) has produced comparable results on mule deer winter ranges in Montana (Gruell 1983).

Long-Term Vegetative Trends

Although game managers have generally accepted the theory of conversion of western ranges from dominance by grasses to shrub dominance, there has been marked disagreement among plant ecologists and range scientists over the extent of the change. Early researchers concluded that much of the Intermountain West currently occupied by sagebrush communities was grassland at the time of settlement (Clements and Clements 1939; Shantz and Zon 1924). Regional studies of plant succession have supported this view

(Christensen and Johnson 1964; Cooper 1960; Cottam and Stewart 1940; Hull and Hull 1974; Stoddart 1941). Conclusions were based on historical descriptions of vegetation and studies of sites that had not been disturbed for long periods.

Others citing historical records, studies of relatively undisturbed sites, and soils analyses have concluded that the sagebrush/grass vegetation type is ecologically stable and its boundaries closely resemble those that existed at the time of settlement by Euroamericans (Tisdale and Hironaka 1981). Blaisdell (1953) reported that before settlement the major part of the upper Snake River Plains was probably an open stand of sagebrush and other shrubs, beneath which was a vigorous stand of perennial grasses and forbs. Vale's (1975) analyses of 29 emigrant journals covering major travel routes through Wyoming, Idaho, Nevada, Oregon, and Colorado, led him to conclude that shrubs (principally sagebrush) visually dominated pristine vegetation. Those holding to the viewpoint of historical dominance by sagebrush believe that sagebrush did not invade grassland on a large scale. Instead, they contend that heavy livestock grazing eliminated or reduced palatable grasses and forbs, and allowed an increase in the size, density, and vigor of sagebrush (Hironaka and others 1969).

EVIDENCE FROM HISTORICAL ACCOUNTS

Because of the disagreements on the presettlement occurrence of sagebrush and bunchgrass in the Intermountain West, I undertook the following analysis of historical accounts of vegetation (appendixes 2 and 3) (see fig. 1 for approximate locations). This analysis differs from others because it distinguishes the vegetation of the plains and semiarid valleys from that of the more productive mountain valleys and slopes. Past interpretations have either focused on a few localized areas or considered vegetation over vast areas encompassing wide variation in site potential.

The early records in appendix 2 indicate that before Euroamerican settlement, sagebrush covered extensive areas of the plains and semiarid valleys. Depending upon geographical location and elevation, average annual precipitation varied between 8 and 15 inches. Sagebrush was particularly abundant on sandy, gravelly, or clayey soils, and on basalt (Bradley 1873; Endlich 1879; McKinstry 1975; Raynolds 1868). Early travelers considered these regions barren or sterile because of the dominance of sagebrush and other semidesert shrubs. Sagebrush was also widely distributed in the driest valleys (8 to 10 inches precipitation) where soils were more productive. Here, surface soil moisture deficiencies apparently limited growth of bunchgrass and favored the deep-rooted sagebrush.

Sagebrush did not dominate plains and semiarid valleys where retention of soil moisture was high, such as the upper Snake River Plains transition zone near the present site of St. Anthony, ID (Bradley 1873). Bunchgrass was conspicuous in these areas, particularly in riparian zones (Endlich 1879; Haines 1971; Raynolds 1868; Simpson 1876).

In contrast to the plains and semiarid valleys, early accounts suggest that vegetation on mountain valleys

and slopes (appendix 3) was visually dominated by bunchgrass. Such sites have good potential for supporting grass because their fine-textured soils have good moisture retention capacity and they receive 10 to 25 inches of precipitation. Much of this land has been converted into irrigated pastures and dryland farms.

Over broad areas that have not been cultivated, comparison of early descriptions of vegetation with current vegetation suggests a conversion from dominance by bunchgrass to woody vegetation. For example, in Montana's Ruby Range, the rolling hills beautifully clothed with bunchgrass described by Russell in 1835 are no longer covered with grass, nor are the hills in the Monida Pass locality dominated by yellow bunchgrass as described by Stuart in 1857. In Wyoming, the middle fork of Owl Creek is still covered by grass (Jones 1875), but the Cottonwood and Gooseberry Creek drainages that were once grass covered are now dominated by sagebrush. In Idaho, sagebrush and juniper are the dominant vegetation on the hills between Bear River and Malad, while sagebrush predominates in the Henry's Lake area. These regions were described as being grass covered in the 1840's and 1870's (Fremont 1887; Hayden 1872). Utah's Mountain Meadows described in 1844 by Fremont and in 1851 by Pratt evidently changed from grass dominance to shrub dominance by 1877 (Cottam and Stewart 1940). In Utah's Cache Valley, dense stands of sagebrush became established in grasslands by the late 1880's (Hull and Hull 1974). The grass cover on the slopes in eastern and central Nevada described in 1859 by Kern is no longer conspicuous, nor is bunchgrass the major vegetal component in the Secret Pass and Emigrant Pass localities of northeastern Nevada. Today, shrubs and cheatgrass comprise the primary vegetation in these regions. Visual dominance of bunchgrass on mountain valleys and slopes was interrupted by sagebrush dominance wherever soil productivity was low. In 1843, while in southwestern Idaho, Fremont (1887) observed:

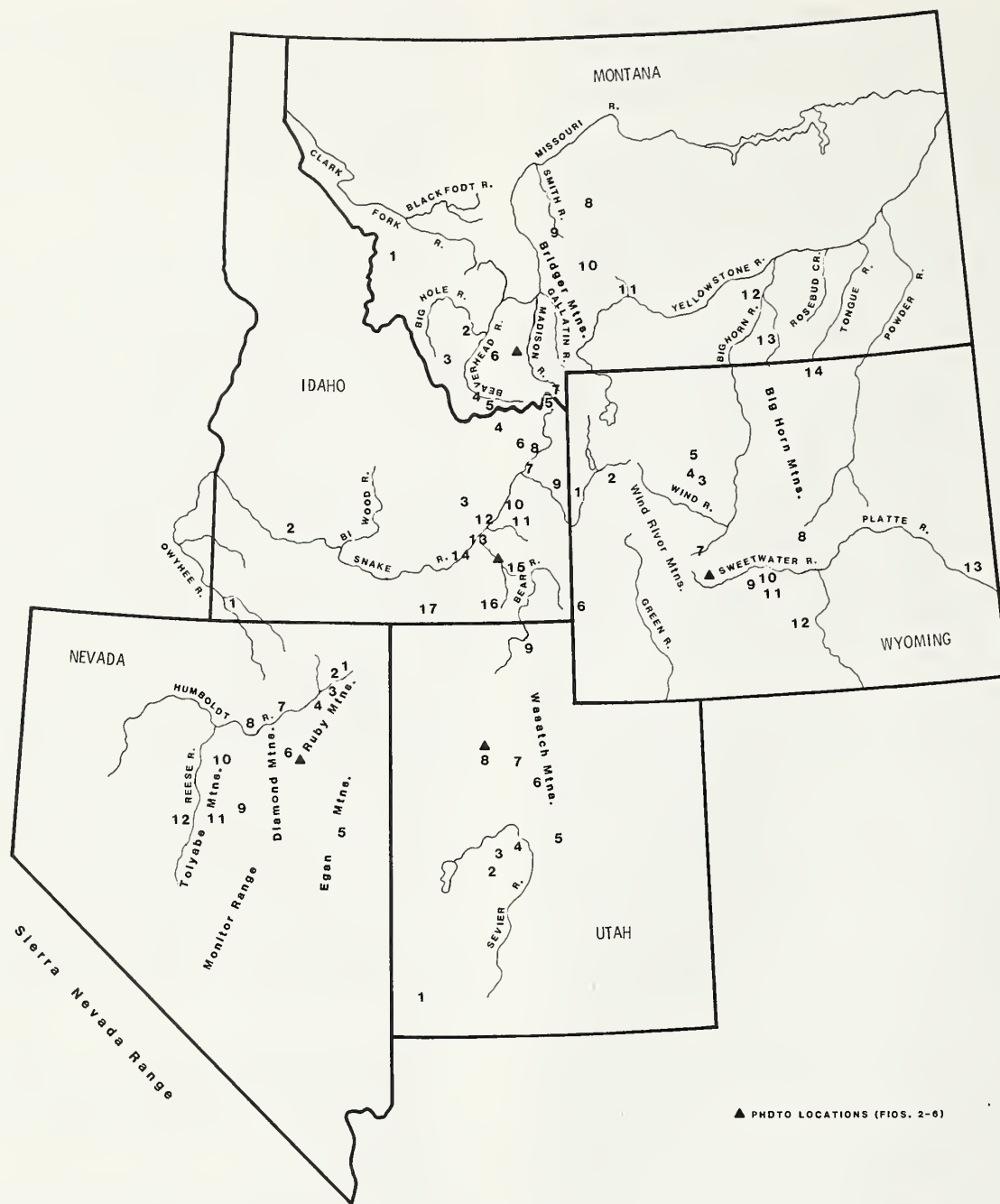
This plant [sagebrush] loves a dry, sandy soil and cannot grow in the good bottoms where it is rich and moist; but on every little eminence, where water does not rest long, it maintains absolute possession.

By inference, Fremont's statement suggests that grasses commonly occupied deep soils. Because sagebrush was capable of growing on these sites, there is reason to believe that it was excluded by fire.

EVIDENCE FROM HISTORICAL PHOTOGRAPHS

Further perspective on the condition of early vegetation in the Intermountain West can be had by comparing historical photographs with matched retakes. This is the only means of visually evaluating long-term vegetal changes over wide geographical areas. Care should be exercised in accepting the original photograph as a reliable measure of the presettlement condition because there is evidence that significant vegetal changes had occurred in some localities by the late 1800's.

Changes in vegetation have been documented by means of photo-retakes in Montana (Phillips 1963;



▲ PHOTO LOCATIONS (Figs. 2-6)

MONTANA

- 1- BITTERROOT VALLEY
- 2- MELROSE VALLEY
- 3- HORSE PRAIRIE
- 4- RED ROCK CR.
- 5- MONIDA PASS
- 6- RUGBY RANGE
- 7- RAYNOLD'S PASS
- 8- LITTLE BELT MTNS.
- 9- SMITH VALLEY
- 10- SIXTEEN MILE CR.
- 11- BIG TIMBER CR.
- 12- HARDIN
- 13- LITTLE HORN CR.

IDAHO

- 1- OWYHEE PLATEAU
- 2- MOUNTAIN HOME
- 3- ATOMIC CITY
- 4- PLEASANT VALLEY
- 5- HENRYS L.
- 6- SNAKE RIVER PLAINS
- 7- REXBURG
- 8- ST. ANTHONY
- 9- TETON BASIN
- 10- RIRIE
- 11- TAYLOR MTN.
- 12- BLACKFOOT
- 13- POCA TELLO
- 14- AMERICAN FALLS
- 15- LAVA HOT SPRINGS
- 16- MALAD
- 17- RAFT R.

WYOMING

- 1- JACKSON HOLE
- 2- GROS VENTRE R.
- 3- OWL CR.
- 4- COTTONWOOD CR.
- 5- GOOSEBERRY CR.
- 6- COKEVILLE
- 7- POPO AGIE R.
- 8- RATTLESNAKE HILLS
- 9- SWEETWATER PLATEAU
- 10- JEFFERY CITY
- 11- CROOK'S GAP
- 12- RAWLINS
- 13- LARAMIE PLAINS
- 14- SHERIDAN

UTAH

- 1- MOUNTAIN MEADOWS
- 2- PAVENT VALLEY
- 3- HOLDEN
- 4- ROUND VALLEY
- 5- EPHRAIM CANYON
- 6- SPANISH FK.
- 7- UTAH L.
- 8- TDOLE VALLEY
- 9- CACHE VALLEY

NEVADA

- 1- THOUSAND SPRINGS
- 2- BISHOP CR.
- 3- WELLS
- 4- SECRET PASS
- 5- STEPTOE VALLEY
- 6- HUNTINGTON VALLEY
- 7- ELKO
- 8- EMIGRANT PASS
- 9- ROBERTS CR.
- 10- SIMPSON PARK RGE.
- 11- BIG SMOKY VALLEY
- 12- REESE RIVER VALLEY

Figure 1.—Locations of sites in appendixes 1 and 2.

USDI, BLM 1979, 1980; Houston 1982; Gruell 1983), Wyoming (Phillips 1963; Progulske 1974; Gruell 1980; Houston 1982), Idaho (Gruell 1983), Utah (Rogers 1982), and Nevada (Gruell 1966). Comparison of the original scenes with modern retakes, spanning 100 years or more, shows expansion of shrub and tree cover at the expense of herbaceous vegetation. The extent of change varies with each site's potential to produce woody plants, disturbances, and amount of elapsed time between photos. Photos retaken in semiarid rangelands after a relatively short interval (about 40 years) showed the least amount of change. In contrast, scenes retaken after 100 years or more on mesic sites showed marked increases in woody vegetation.

Five photo pairs (figs. 2-6) were selected as representative of successional changes in vegetation types within the mountain valley and slope environments comprising mule deer habitats. The criteria for photo selection were visual clarity and length of time elapsed since the date of the original photograph. The early scenes in Montana, Wyoming, and Nevada are from my past studies. Those in Utah and Idaho were supplied by others. Pre-1900 photographs were preferred because they allowed evaluation of vegetation changes over a relatively long time period. Nonetheless, the "original photographs" probably reflect successional advances beyond what would be expected prior to occupancy by Euroamericans when fire was the major disturbance factor.

Vegetative cover types represented by historical photographs include:

Figure 2. Montana - Douglas-fir/bunchgrass

Figure 3. Wyoming - Lodgepole pine/limber pine/
sagebrush/bitterbrush

Figure 4. Idaho - Juniper/bitterbrush

Figure 5. Utah - Juniper/sagebrush

Figure 6. Nevada - Pinyon/juniper/mahogany

Analysis of these early photographs (figs. 2a-6a) shows that:

1. Smooth slopes characteristically were covered by grasses or a mixture of shrubs and grasses.
2. Crown-sprouting or cloning shrubs and trees were in an early seral condition.
3. Conifers were largely restricted to ridges, rock outcrops, or mesic sites.

4. Conifer cover was sparse in the canyon bottoms.

By comparison, the analysis of the modern retakes (figs. 2b-6b) shows that:

1. Smooth slopes and canyon bottoms have often become dominated by conifers.
2. Crown sprouting or cloning shrubs and trees such as willow, aspen, and chokecherry have increased in frequency and size.
3. There has been an increase in fire-sensitive shrubs preferred by mule deer including sagebrush, bitterbrush, and curlleaf cercocarpus (*Cercocarpus ledifolius*)(curlleaf mountain-mahogany).

Although not apparent in the photographs, important browse plants including bitterbrush (fig. 4b), sagebrush (fig. 5b), and mountain-mahogany (fig. 6b) are being displaced by conifers. With advancing succession, browse plants pictured in figs. 4b and 6b are also being lost as a result of defoliators and boring insects.

Historical narratives and photographic evidence suggest that, before settlement by Euroamericans, bunchgrasses were the predominant vegetation in mountain valleys and on slopes that comprise the great majority of mule deer habitats. The relative distribution of bunchgrass and sagebrush seems to have been strongly influenced by available soil moisture. In general, the mountain valleys and slopes have a higher potential for growth of bunchgrasses than plains and semiarid valleys because of more productive soils and greater precipitation. Bunchgrass production on plains and semiarid valleys was apparently limited by insufficient soil moisture resulting from low precipitation, coarse or clayey soils, and persistent drying winds. These environments were characteristically covered by an expanse of sagebrush, except for stands of bunchgrass wherever soils were suitable.

These interpretations are in disagreement with those who have concluded that the early landscape was dominated by sagebrush. Supporters of the sagebrush dominance theory (Vale 1975) have cited journals covering primary travel routes through plains and semiarid valleys where sagebrush is the indicated climatic climax vegetation. This evidence does not properly consider mountain valleys and slopes that comprise a significant part of the landscape.



Figure 2a.—1871. An east-northeast view (elevation 6,000 ft) up Alder Gulch above Virginia City, MT. Placer mining following discovery of gold in 1863 caused extreme disturbance of canyon bottom. The south facing bluebunch wheatgrass covered slope at left supports a few mature Rocky Mountain juniper in rock outcrops. Juniper and Douglas-fir regeneration is evident. Conifers on north facing slope at right are Douglas-fir. Stumps in area indicate light cutting of trees. Wildfires had been relatively frequent in this locality. Examination of two fire-scarred stumps showed evidence of four fires before 1871. Photograph by W. H. Jackson, courtesy of Montana Historical Society.



Figure 2b.—July 28, 1981. (110 years later.) The large Douglas-fir in left foreground (arrow) is the same one pictured in original scene. Regeneration of Douglas-fir and Rocky Mountain juniper on this slope has produced a marked change. Canyon bottom now supports various shrubs and trees including aspen, narrow leaf cottonwood, willow, and chokecherry. North slope is densely covered by Douglas-fir. Photograph by G. E. Gruell.



Figure 3a.—August 1870. A northwest view of Chief Washakie's Shoshone encampment on Willow Creek; Wind River Mountains, WY (elevation 8,200 ft). Shrubs in foreground appear to be sagebrush. Snags in distance show evidence of slopes having been swept by fire. W. H. Jackson photograph, courtesy of Colorado Historical Society.



Figure 3b.—July 27, 1967. (97 years later.) Scene shows more landscape at left than original. Improved soil moisture from irrigation favored growth of herbs and willow in bottom-lands. Slopes in distance support lodgepole pine and limber pine. A mixture of sagebrush and bitterbrush covers bench on right. Photograph by G. E. Gruell.



Figure 4a.—July 1907. Looking west across Mink Creek at a point about 6 miles from its confluence with the Portneuf River in southeastern Idaho (elevation 5,400 ft). Juniper on distant slopes are restricted to south exposures where they were protected from frequent presettlement fires. The dark shrubs are bitterbrush that appear to be closely grazed. Note predominance of herbs in foreground. Prof. Toumey photograph, courtesy Douglas Turner.



Figure 4b.—September 8, 1982. (75 years later.) In the absence of fire, juniper has markedly increased by spreading to deeper soils. Bitterbrush has also increased in density and size. Arrow points to expansion of chokecherry and other shrubs. The general increase in woody vegetation is illustrated in foreground. Photograph by G. E. Gruell.



Figure 5a.—1901. Facing north from a point 3 miles east of Skull Valley Indian Reservation near road to Dry Canyon, Stansbury Mountains, UT (elevation 5,900 ft). Benchlands support Utah juniper that are largely confined to areas of shallow soil. Stumps indicate a low level of cutting. Big sagebrush is the predominant shrub. Gilbert photograph, courtesy USGS.



Figure 5b.—September 3, 1976. Juniper has increased in all areas, and young trees and seedlings are abundant. The increase has been greatest in the areas of low slope angle and least on the mountain slopes at right. Photograph by Gary Rogers, photograph courtesy of Gary Rogers and the University of Utah Press.



Figure 6a.—1868. Looking east-southeast down canyon from a point about 1.5 miles above Flyn and Hager Spring in Ruby Valley, NV (elevation 7,500 ft). Open slope in midground appears to be covered by herbs and snowberry. Curlleaf mountain-mahogany, pinyon, and juniper are confined to rocky areas where they have been protected from fire. Note regenerating aspen on lower-left edge of photo (arrow). Timothy O'Sullivan photograph, courtesy USGS.



Figure 6b.—July 31, 1982. (114 years later.) The absence of fire for over 114 years has allowed woody vegetation to proliferate. Aspen at bottom-left have matured (open arrow). Photograph by G. E. Gruell.

	Poor or/ dry sites	Better or/ moist sites
Climatic climax ^a	Sagebrush	Sagebrush
Pre-1900 Fire Climax	Sagebrush	Bunchgrass

^aFound on modern "undisturbed sites" where fire has been suppressed.

Figure 7.—Postulated bunchgrass and sagebrush occurrence as influenced by site potential and disturbance

The sagebrush dominance theory has also been arrived at by study of relatively "undisturbed" or "relic" areas that are approaching a "climatic climax" condition. This approach does not consider prior history of disturbance. It assumes that these sites represent presettlement conditions, but overlooks evidence of frequent fires and hence the fire climax that prevailed prior to settlement (fig. 7). Post-1900 measurements invariably represent a vegetal state that had been altered by extreme livestock grazing and a prolonged period of fire's absence. Consequently, the amounts of fire-sensitive sagebrush and herbs recorded are not indicative of presettlement vegetative conditions. Tisdale and Hironaka (1981) recognized the potential of fire to create temporary grasslands within the sagebrush/grass regions. As will be discussed in more detail, this may be why grasslands prevailed across the more productive landscapes prior to settlement.

Reasons for Vegetative Changes

Several reasons have been advanced for the change from grass to shrub dominance. In the Southwest, Hastings and Turner (1965) concluded that a shift to woody vegetation was climatically influenced. But, Cooper (1960) saw no evidence of a large-scale climatic change in the past 1,000 years. Likewise, tree ring analysis in eastern Oregon by Keen (1937) revealed no general trend toward wetter or drier years during the past 650 years.

Two of the more probable causes for vegetal change are livestock grazing and fire. Both of these factors will be examined. Understanding their respective roles should help determine where they fit in future management of mule deer habitats.

INFLUENCE OF LIVESTOCK GRAZING

Many investigators studying mule deer have agreed that on western grass ranges the grazing of domestic livestock triggered growth of successional food plants preferred by deer (Leopold 1950; Julander and Low 1976; Longhurst and others 1952, 1981; Salwasser 1976; Urness 1976). Intensive grazing of rangelands occurred from the mid-19th-century settlement up to (in some

cases) the present time. The period of heaviest grazing was generally from 1880 to 1930 (Urness 1976). Leopold (1950) concluded that overgrazing in central and western California allowed expansion of chaparral at the expense of grassland and oak woodland. He suggested that similar shrub invasions occurred widely throughout the Great Basin as a result of past grazing. Longhurst and others (1976) reported that east of the Sierra and Siskiyou Mountains, and in the Great Basin range type, early cattle and sheep impacts were primarily responsible for reduction of native perennial grasses and establishment of shrubs. This conclusion was also reached for the 11 western States (Longhurst and others 1981). Severe depletion of Utah's grasslands as a result of excessive domestic livestock grazing gave rise to an abundance of browse-producing shrubs (Frischknecht and Plummer 1955; Julander and Low 1976). For example, important species such as bitterbrush, sagebrush, curleaf mountain-mahogany, and rabbitbrush (*Chrysothamnus* spp.) increased in abundance (Julander 1962; Urness 1976; Salwasser 1976).

Extreme soil disturbance and depletion of herbaceous plants were believed to be primary factors in establishment of shrubs and trees. Serious reduction or virtual elimination of competing perennial grasses and palatable forbs especially contributed to shrub and tree establishment (Julander 1962).

INFLUENCE OF FIRE

There is worldwide evidence that fire has been a major perturbing factor affecting plant succession over millennia (Stewart 1951; Pyne 1982). Generally, wildlife biologists and others associated with mule deer management have not fully appreciated the past role of fire. A few investigations, however, have suggested that exclusion of fire favored a shift to shrub dominance, thus allowing mule deer increases (Harper 1968; Julander 1962; Salwasser 1976; Urness 1976). But neither evidence of past fires nor the ecological role of fire has been discussed.

An understanding of fire history and fire ecology is essential to interpreting long-term trends in vegetation. Questions include: How often did early fires burn? How large were they? How did these fires affect vegetation? How did Euroamerican settlement affect fire frequency and size? Has the absence of fire influenced growth of vegetation?

Early Fire Occurrence.—In the scientific and historical literature, I found 145 published accounts of early-day fires in Montana, Wyoming, Idaho, Utah, Nevada, and eastern Oregon (Gruell 1985b). This is by no means an exhaustive listing. The frequency and size of early fires seem to have varied, depending on topography, potential ignition source, weather, and fuels. Denig (Ewers 1961), Catlin (1891), and Havard (1878) report that extensive fires swept the grasslands of central and eastern Montana every year during the period 1832 to 1877. In forested regions of Montana, very large fires occurred during exceptionally dry years such as 1889 when about 530 mi² burned on the Lewis and Clark Forest Reserve, including portions of the Lewis and Clark, Flathead, and Lolo National Forests (Ayres 1901). Elsewhere, extensive

fires were reported in 1834 in western Idaho and eastern Oregon by Captain Bonneville (Todd 1961) and by Captain Nathaniel Wyeth (Young 1899); in 1875 and 1878 in southeastern Idaho by Beaver Dick Leigh (Thompson and Thompson 1982); and in western Wyoming in 1879 by Thomas Moran (Fryxell 1943). Grass-covered valleys and uplands in southern Idaho, northern Utah, and south-central Montana burned frequently (Gruell 1985b). In contrast, Bonneville's observations in 1832 suggest that fire was rare in areas like the Laramie Plains in Wyoming, where sparse fuels would not carry fire (Todd 1961). Sparsely vegetated regions in the drier sagebrush valleys also yield few early reports of fire.

The probability of fires occurring at lower and middle elevations was strongly influenced by the level of Indian activity. Of the 145 accounts of fire found in the literature, 41 percent were attributed to ignitions by Indians (Gruell 1985a). The apparent reasons for setting fires included communication, warfare, hunting, forage enhancement, food gathering, and clearing vegetation (see Barrett 1981). Escaped fires were undoubtedly common. Lightning also caused many fires, especially at higher elevations, although the historical literature surprisingly makes little mention of this. Fires were sometimes also carelessly ignited by fur trappers during the presettlement era (Haines 1971; Stevens 1855). During the late 1800's prospectors apparently caused many fires, particularly in the mountains where mining was occurring (Leiberg 1904).

Fire history studies based on analysis of fire-scarred trees have provided quantitative information on past fire periodicities in the Northern and Middle Rocky Mountains of Montana, Wyoming, Utah, and the Owyhee Plateau of Idaho. These studies confirm that fires were frequent in semiarid regions of the Intermountain West. Average pre-1900 fire intervals were 4 to 20 years in ponderosa pine/Douglas-fir forests in the Bitterroot Valley of western Montana (Arno and Peterson 1983). Fire scar dates from higher and cooler Douglas-fir/mountain big sagebrush (*Artemisia tridentata vaseyana*) ecotones in Yellowstone Park and southwestern Montana suggest fire intervals varied from 20 to 40 years (Houston 1973; Arno and Gruell 1983). Shorter intervals evidently prevailed in grassland-aspen associations. For example, fire-scarred aspen in Ephraim Canyon, UT, showed a mean fire interval of from 7 to 10 years during the period 1770 to 1875 (Baker 1925). Burkhardt and Tisdale (1976) report presettlement fire intervals in southwestern Idaho sagebrush-grass/western juniper (*Juniperus occidentalis* ssp. *occidentalis*) ecotones were about 11 years. In general, fires have been less frequent (50 to 300 years or longer) in moist or subalpine regions of the Northern Rockies (Loope and Gruell 1973; Romme 1979; Arno and Davis 1980; Barrett 1982).

Fire Effects on Vegetation.—A few early travelers recognized that fire promoted grasses and suppressed shrub development (Gruell 1985b). In southwestern Montana, Mullan (1855) wrote: "In many places the valley has been burnt over, and the young, green grass is now growing abundantly."

In August 1843, on the lower Bear River in Utah, Fremont (1887) observed the presence of young willows. He noted that older trees were rarely found because Indians burned the plains to produce better grass.

Cooper (1961) and Daubenmire (1968) report that fire enhances grass production and suppresses woody plants. Fire in grasslands generally promotes seed production, germination, and establishment of grass seedlings (Vogl 1979).

Fire severity has a strong influence on the recovery rate of grasses. Severity is primarily influenced by fuel loading and season of the fire. Study of grass response following a late-summer prescribed fire in dense sagebrush on the upper Snake River Plains resulted in slow recovery of fine bunchgrasses such as Idaho fescue (*Festuca idahoensis*) and needle-and-thread grass (*Stipa comata*) where the burn was hot (Blaisdell 1953). Coarse grasses including thickspike wheatgrass (*Agropyron dasystachyum*), plains reedgrass (*Calamagrostis montanensis*), and bluebunch wheatgrass (*Agropyron spicatum*) recovered rapidly. Burning of grassy fuels containing little woody material often results in rapid recovery of bunchgrasses because the residence time of the fire is short and temperatures are not extreme.

Big sagebrush is readily killed by fire (Blaisdell 1953). It is an important component in the diet of wintering mule deer (Bayless 1975; Leach 1956; Richens 1967), and it supplies needed cover. The importance of this plant to mule deer underscores the need to understand fire relationships. In the more productive mountain valleys and slopes that comprise most mule deer habitats, vegetation burned frequently, thus inhibiting the development of sagebrush. The historical record suggests that the presence of sagebrush is largely dictated by the elapsed time since the last fire. Fire intervals of 1 to 20 years would relegate sagebrush to widely scattered plants or patches depending on topography. Expansive fire-climax grasslands with little sagebrush would have prevailed on smooth topography where fuel continuity allowed fires to carry over extensive areas. Because of the scattered distribution and low occurrence of its seed source, sagebrush recovery potential would have been much slower than today.

The effect of early fires on bitterbrush, an important winter forage of mule deer, was apparently one of inhibiting stand establishment and development. Bitterbrush is considered fire sensitive (Nord 1965; Wright and others 1979), but it responds differently to fire because of genotypic variations (Wright and others 1979; Bunting and others 1985). Decumbent forms sprout more readily after top removal than do open growth forms. Plant mortality seems to be influenced by one or more factors including fire intensity (Blaisdell 1953), phenology (Mueggler and Blaisdell 1958), soil moisture (Nord 1965), and soil texture (Driscoll 1963). A medium-intensity prescribed fire through antelope bitterbrush in northwestern Montana during the spring resulted in a 33 percent loss of plants (Bumstead 1971). Late-summer prescribed burns on eastern Idaho sagebrush ranges killed two-thirds of the bitterbrush (Pechanec and others 1954). Summer wildfires of moderate intensity in eastern

Oregon have removed entire stands of bitterbrush (Countryman and Cornelius 1957).

Fire frequency appears to have been an important factor affecting presettlement distribution and density of bitterbrush. An extreme effect is suggested in Oregon where experimental annual spring burning beneath ponderosa pine over a 21-year period left only a few scattered, stunted plants in the larger openings (Weaver 1961; 1967). Historical photographs in the Bitterroot Valley of western Montana show evidence that frequent fires (7-year intervals from 1600 to 1900) severely limited development of bitterbrush (Gruell and others 1982). Considering the sensitivity of bitterbrush seedlings to fire, it is highly probable that a fire frequency of 5 to 20 years would result in sparse distribution and low density of bitterbrush.

Curlleaf mountain-mahogany, a weak sprouter, is an important forage plant for wintering mule deer. Investigations suggest that fire effects differed, depending upon whether mountain-mahogany was seral to conifers or represented the potential climax vegetation (Gruell and others 1985). For example, mountain-mahogany associated with moist subalpine fir (*Abies lasiocarpa*) habitat types was subjected to infrequent, stand-destroying fires, after which new stands of mountain-mahogany developed from seedlings. In contrast, mountain-mahogany growing in drier communities was confined to rocky sites or thin soils where sparse fuels limited fire spread. These sites afforded protection for mountain-mahogany. Expansion of mountain-mahogany was restricted because seedlings were unable to become established on deeper soils where fuel accumulations resulted in frequent fires.

Before settlement, grass or sagebrush/grass regions now covered by juniper and pinyon/juniper woodlands were subjected to frequent wildfires (Burkhardt and Tisdale 1976; Leopold 1924). Fires restricted trees to ridgelines or sites where fuels were sparse (fig. 4).

There is much evidence that frequent fires in the pinyon-juniper types can maintain a grassland setting, and conversely that lack of fire will result in development of woodlands (Arnold and others 1964; Barney and Frischknecht 1974; Dwyer and Pieper 1967; Jameson 1962). Recurrent fires retard juniper encroachment (Gartner and Thompson 1972; Wedel 1957), and young juniper trees up to 4 feet high are highly susceptible to fire mortality (Dwyer and Pieper 1967; Jameson 1962).

Presettlement fires apparently had varying effects on crown-sprouting shrubs and trees such as ceanothus (*Ceanothus* spp.), willow (*Salix* spp.), mountain maple (*Acer glabrum*), Gambel oak (*Quercus gambelii*), aspen (*Populus tremuloides*), chokecherry (*Prunus emarginata*), and serviceberry (*Amelanchier* spp.). Postfire response depended upon plant species, fire severity, fire periodicity, and site conditions. Historical photographs and recovery and growth rate studies suggest that shrub species growing in ponderosa pine, in dry Douglas-fir, and in nonforested environments where grass fuels were abundant were suppressed by frequent surface fires (Cooper 1961; Gruell and others 1982; Gruell 1983). In contrast, in moist conifer forests infrequent stand-replacement fires and moderate intensity thinning fires

removed conifer competition and allowed development of early successional vegetation.

Reduced Fire and Plant Response.—Fire's influence on vegetation in the Intermountain West was dramatically reduced following Euroamerican settlement. This change resulted from several interrelated factors (Gruell 1983). Of primary importance was relocation of Indians from their ancestral territories to reservations, thus removing a major ignition source. Introduction of domestic livestock and yearly consumption of fine fuels checked the possibility of extensive spreading fires. Development of irrigated pastures and construction of roads broke up fuel continuity, thereby limiting fire spread. By the early 1930's, with development of an effective fire suppression system, fire potential was substantially reduced.

The absence or marked reduction of fire over extensive areas has favored the development of fire-sensitive plants, including sagebrush, bitterbrush, and curlleaf mountain-mahogany. Big sagebrush has increased manifold on productive sites in Montana (Gruell 1983), Wyoming (Gruell 1980), and Nevada (Gruell 1966). In southwestern Montana, fire scar data suggest that this trend coincided with a fire-free period of about 80 to 130 years (Arno and Gruell 1983). On the Klamath Indian Reservation in Oregon, Weaver (1957) reported that expanded distribution and increased density of bitterbrush resulted from 40 to 50 years of fire exclusion. In western Montana, a great increase in bitterbrush was found in a ponderosa pine forest where wildfire has been excluded since about 1900 (Gruell and others 1982). Hazeltine and others (1961) report that establishment of bitterbrush stands in Elko County, NV, in about 1890 resulted from livestock reductions following the severe winter of 1889-90. There are strong implications, however, that heavy livestock grazing had eliminated the possibility of fire, thus allowing bitterbrush to proliferate.

In fire's absence, curlleaf mountain-mahogany has increased greatly on productive sites that had been subjected to frequent surface fires (Gruell and others 1985). Most mountain-mahogany stands on deeper soils are less than 125 years old and have increased on these sites as a result of removal of fine fuels by livestock and absence of fire (Scheldt 1969; Dealy 1975; Gruell and others 1985).

Burkhardt and Tisdale (1976) reported that invasion of western juniper into a big sagebrush community on the Owyhee Plateau appeared to be directly related to a marked reduction in fires starting in the 1870's. At Mountain Meadows, UT, Cottam and Stewart (1940) recorded a 500 percent increase in Utah juniper (*Juniperus osteosperma*) between 1862 and 1934. They concluded that this dramatic increase was best explained by the elimination of grass competition by livestock. Subsequent studies such as Burkhardt and Tisdale (1976) would suggest, however, that the absence of fire was the primary reason for juniper increases.

The photo pairs in figures 2 through 6 show an increase in the number and size of fire-sensitive shrubs and trees as well as crown sprouting shrubs and trees. The same vegetal trend is documented in other photographic comparison studies cited previously. As suggested by fire history studies, historical accounts of fire,

and aging of shrubs, this trend is largely the result of lack of fire over long periods.

Summary—Hypothesis 1

The case for hypothesis 1 may be summarized as follows: The irruption of mule deer that occurred early in the 20th century was too pronounced, widespread, and persistent to be an ordinary population fluctuation and therefore was probably due to some dramatic ecological change. The quality of mule deer habitat is determined by the abundance of nutritious forage, a high percentage of which is in the form of palatable shrubs, and stands of small trees to provide cover and shelter. Prior to settlement, frequent fires favored grasses and inhibited widespread development of shrubs and trees, except on rocky or moist sites. Settlement brought pronounced disruption of existing plant communities. Intensive grazing suppressed and sometimes destroyed the grasses, allowing an invasion of forbs and woody plants. Consumption of fuels by livestock, elimination of Indian ignitions, development of irrigated croplands, roads, and communities, and the advent of organized fire suppression brought a marked reduction in numbers, size, and intensity of fires. Thus, succession from grasses to forbs and woody plants was allowed to proceed. Eventually, a new assemblage of herbs, shrubs, and trees constituted mule deer habitat far superior to the pristine dominance of grasses; hence mule deer populations irrupted throughout the Intermountain West.

HYPOTHESES 2 THROUGH 4

Hypothesis 2: Conversion of Conifer Forests to Seral Shrubs

Large increases in mule deer populations have been attributed to conversion of conifer forests to successional shrubfields. Logging and fire on summer ranges in the Sierra Nevada Mountains benefited mule deer by opening up conifer stands and allowing midsuccessional shrubfields to proliferate (Longhurst and others 1952; Salwasser 1976). Pengelly (1963) concluded that logging and fire in Northern Rocky Mountain Douglas-fir/ponderosa pine forests temporarily increased deer forage. In this region, a noticeable increase in mule deer numbers and harvest was observed on timberlands during the 1950's. Lyon (1969) likewise reported that unusually large fires in the Northern Rocky Mountains in 1910 and 1919 created thousands of acres of seral, high-quality brushfield habitat. Deer and elk populations increased in the favorable environment and reached unprecedented highs during the early 1940's.

The cause and effect relationship between abundant, high-quality forage and increased numbers of mule deer is widely accepted. Subjective evidence seems to support the premise, although there is little quantified data that the opening of dense forests by logging and fire resulted in improved forage conditions and increased deer populations.

A majority of mule deer habitats in the Intermountain West, particularly those comprising winter ranges, are situated on shrublands, or semiarid woodlands support-

ing juniper, pinyon pine (*Pinus* spp.), Douglas-fir, limber pine, or ponderosa pine. Large-scale commercial cutting took place at various locations during the period 1860 to 1900 in support of mining operations. A noteworthy example is central Nevada where great quantities of pinyon and juniper were cut to fuel kilns for processing ore and for other needs (Young and Budy 1979; Lanner 1981). Selective cutting for fencing, firewood, and lumber also took place in many localities in the Intermountain West. Careless ignitions often followed cutting operations. Where heavy cutting and fire took place, the disturbance provided a stimulus for regeneration of forage and cover. The absence of fire following disturbances in these ecosystems was an important factor in enhancement of forage and cover because it allowed plants to reach a productive age. Mule deer populations in these ecosystems did not peak until 30 to 70 years after disturbance.

In summary, hypothesis 2—conversion of coniferous forests to shrubs—can be substantiated for commercial forest types that were cut and burned or were swept by large wildfires after the turn of the century. Large-scale cutting of pinyon/juniper and selective cutting of other trees in numerous localities is also consistent with this hypothesis. Hypothesis 2 is not applicable to dry forests and shrublands of the Intermountain West where little or no cutting of conifers occurred because of their sparsity, or absence, or great distance from settlement. Because these lands comprised a large majority of early mule deer habitat, this hypothesis has limited applicability.

Hypothesis 3: Conservation Measures and Predator Control

Leopold and others (1947) concluded from a survey of overpopulated deer ranges in the United States that:

Buck laws, predator control, and over-large refuges, working in combination to allow undue multiplication of breeding females, seem to be the predisposing causes of irruptive behavior.

At the turn of the century, mule deer population levels were so low that there was widespread support for conservation measures. Population reductions had been particularly heavy where large numbers of people were drawn by prospecting for gold. Homesteaders also exploited mule deer, hunting them yearlong, before the advent of game laws. Near some army outposts, heavy hunting contributed to mule deer exploitation.

After game laws were established in the latter 1800's, depletion of mule deer continued because of minimal enforcement. In Utah, a law in 1908 prohibited hunting of deer and other big game for 5 years (Rasmussen and Gaufin 1949). This step was followed by restrictive open seasons. Similar sequences of laws occurred in Nevada, Idaho, Montana, and Wyoming.

In the early 1900's, "the buck law" was enacted to protect breeding females. This regulation was in effect during the years of mule deer population increases and was rescinded in the 1950's after herds had reached peak levels. Exemption of does from hunting, either by buck laws or by large closed areas for considerable periods,

resulted in population irruptions (Leopold and others 1947).

During the first two or three decades of this century when deer herds were at low numbers, numerous game preserves were established to protect big game. By 1925, 11 preserves had been set up on some of the more favorable deer and elk ranges in Utah (Rasmussen and Gaufin 1949). Hunter and Yeager (1956) felt that game preserves were of vital significance in the reestablishment of herds in the western States.

Control of predators to protect livestock has also been identified as a predisposing cause of mule deer irruptions or population increases (Leopold and others 1947; Rasmussen and Gaufin 1949). It was reasoned that all western deer irruptions followed, and none preceded, the initiation of Federal predator control of the public lands in about 1910. These United States irruptions had coincided with greatly reduced predation by wolves (*Canis lupus*) and mountain lions (*Felis concolor*).

As Connolly (1978) discusses, some authors have discounted the premise that control of predators allowed mule deer to increase. They reasoned that, although substantial numbers of mule deer, especially fawns, are taken by predators, predation was not limiting to deer numbers. Caughley (1970) argued that habitat changes rather than predator control were probably responsible for population increases on the Kaibab Plateau in Arizona. Keith (1974) disagreed with this view by maintaining that predation could be a significant regulator of natural ungulate populations.

The relative effects of predation on mule deer populations may have varied regionally. Fish and game departments in Arizona and New Mexico have felt that predators offer definite limitations to herd increases, while departments in other States and Canadian Provinces concluded that predators have no basic influence on maintenance of mule deer numbers (Hunter and Yeager 1956).

There are numerous accounts of specific ungulate populations whose numbers or growth rates were thought to be limited by predation. But of 31 reports in North America summarized by Connolly (1978), only four refer to mule deer. In these cases, the coyote (*Canis latrans*) was either the sole predator or a copredator in combination with the bobcat (*Lynx rufus*). Salwasser (1976) reports that coyotes eat deer, and fawns in particular. High predation rates of coyotes on young fawns have been documented (Trainer 1975; Craiger and Cockle 1981). Also coyote control has resulted in increased fawn survival (McMichael 1970; Robinette and others 1977). Coyotes have accounted for significant losses of adult deer on some winter ranges (Richens 1967).

Although coyotes kill mule deer and have been reported to reduce populations in various localities, there is a question whether coyote predation has been instrumental in suppressing mule deer populations over broad areas. Wagner (1978) points out that deer increases in the West took place in the face of heavy coyote populations. Leopold and others (1947) discounted the coyote as an effective deer predator because many deer irruptions occurred in the presence of numerous coyotes. Salwasser (1976) believes that coyotes are a

proximate factor behind fluctuations in the California-Nevada interstate mule deer herd.

In addressing the predation issue, Connolly (1978) concluded that because ungulate irruptions typically followed suppression of large predators concurrently with human modification of habitats, the relative roles of predator control and habitat modification in promoting ungulate irruptions cannot be assessed. To the contrary, I believe that there is sufficient information to rate the relative importance of predator control and habitat modification in mule deer irruptions.

There is widespread acceptance that ungulate populations are unalterably tied to habitat quality. Other factors being equal, poor habitats produce few animals, while quality habitats produce many animals. Evidence already presented in this paper suggests that many presettlement habitats had a low capacity for producing mule deer because of frequent fires. These relatively stable environments of low-carrying capacity were not capable of supporting high densities of mule deer. Following settlement in the mid- to late-1800's, mule deer habitats and populations were exploited and numbers were further depressed. The probability of mule deer populations irrupting on these marginal ranges as a result of predator control seems remote. As Hornocker (1976) points out from studying mountain lion predation:

If suitable habitat is not available for prey species, then no amount of predator control will bring about flourishing populations of that prey species.

The bulk of evidence strongly suggests that mule deer increases in the Intermountain West were complemented by predator control. Predator control coincided with mule deer habitats that had been unintentionally enhanced by man's activities. Where there were relatively high numbers of predators to prey, predator removal would have allowed accelerated increases in mule deer.

The evidence does not support the contention that conservation measures and predator control were solely responsible for mule deer population increases. This conclusion overlooks the role of habitat in influencing populations. It seems evident that mule deer would not have been able to reach the levels achieved by the 1950's had habitat conditions remained at a low level of productivity, as was the situation before settlement. There seems to be little doubt that improved forage and cover resulted in widespread optimization of mule deer habitat. This not only allowed mule deer populations to increase on existing habitat, but to expand into areas that previously were poor habitat.

Hypothesis 4: Reduction in Livestock Numbers

Some authors have reported that establishment of grazing systems on livestock ranges and reduction of livestock numbers contributed to improved forage conditions for mule deer. They reason that improved forage conditions in conjunction with other factors allowed mule deer populations to increase (Rasmussen and Gaufin 1949; Salwasser 1976).

Before Euroamerican settlement, mule deer competed for forage with other native ungulates and small mammals. Differences in habitat preferences tended to separate populations, thereby minimizing interspecific competition.

The introduction of livestock into the Intermountain West in the 1860's resulted in unprecedented competition for forage. Wagner (1978) reports that sheep, not including lambs, in the 11 western States reached a level of nearly 20 million by 1895, and then varied between 20 and 30 million for the next 50 years. Turning stock onto spring ranges when plants were in the formative stages of development was particularly harmful and led to widespread destruction of vegetation. The practice of grazing sheep and cattle in common resulted in the overuse of forage species. Bunchgrasses were especially impacted. By the mid-1930's, the forage resource had been heavily depleted. The level of depletion varied latitudinally from moderate in northern Montana to severe in most of Nevada and Utah (Clapp 1936). In different parts of the West, grazing capacity for livestock in the early 1930's was estimated to be 60 to 90 percent less than in pioneer days (McArdle and Costello 1936). The sagebrush-grass type was particularly impacted by grazing. Marked increases in sagebrush were noted as a result of removal and weakening of grass competition.

After excessive domestic grazing during the late 1800's and early 1900's, mule deer populations began to increase in localized areas despite heavy use by livestock. Mule deer population irruptions were reported in parts of Nevada and Utah in the 1930's and in the mid-1940's in Idaho (Leopold and others 1947). Julander (1962) addressed the question of how large populations of mule deer could build up on depleted range in Utah. He concluded that a great increase in woody shrubs provided habitat that permitted an extremely high buildup of deer numbers. Because of increased browse production, population peaks were believed to be much higher than could have been reached on presettlement ranges.

Livestock reductions starting in the early 1920's were instrumental in providing more usable habitat for mule deer. Much of the improvement took place on National Forests which comprised a large segment of mule deer habitat in the West. Here, sheep numbers were reduced from more than 8 million in 1918 to about 2.5 million by 1960 (Wagner 1978). This marked reduction resulted in fewer sheep bands per allotment, thus allowing herders to graze sheep in more accessible areas while leaving the steeper slopes only lightly grazed or untouched. This increase in forage availability in mountain habitats was apparently favorable for mule deer population increases.

Cattle numbers in the 11 western States have steadily increased from about 3 million in 1870 to about 23.5 million in 1975 (Wagner 1978). Most of this increase, however, was due to a shift from open

range to feedlots and private pastures. Cattle numbers on National Forests have not followed the same trend. Records show a decline from nearly 9 million in 1918 to about 5.3 million in 1973 (Wagner 1978). It would appear that this decline was favorable to deer, particularly in earlier years on ranges where stocking was great and competition was excessive.

Although there is less overlap between the diets of cattle and deer compared to sheep and deer, forage competition can result, particularly in arid regions where forage is limited (Gallizioli 1977). Conversion from sheep to cattle on many allotments since the early 1960's has tended to concentrate use on riparian areas and more gentle terrain that is important mule deer habitat. Longhurst and others (1981) suggest that this trend has been detrimental to mule deer because of increased competition for forage. This apparently has occurred in many localities. Conversely, benefits to mule deer also occurred on steeper terrain unsuitable to cattle use where the forage resource improved due to reduced grazing pressure by domestic livestock.

The combined evidence suggests that reductions in sheep grazing allowed increased availability of forage that complemented mule deer population increases. Conversion from sheep to cattle on public lands seems to have had a variable effect depending upon topography, water availability, and stocking rates. Overall the effect was positive because of less overlap in diets and a reduction in competition for forage on steeper terrain.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Of four hypotheses that may have favored mule deer population increases between the early 1930's and mid-1960's, the most likely is that successional changes in deer habitat were primarily responsible. Much evidence shows that woody plants preferred by mule deer markedly increased in mountain valleys and on slopes of the Intermountain West following settlement. Succession to shrubs and trees seems to have mainly resulted from livestock grazing and a marked decrease in fire occurrence. Conservation measures, predator control, and livestock reductions all complemented the habitat improvement that led to population increases.

Toward the end of the 20th century, the condition of mule deer habitats in the Intermountain West varies widely, depending upon site potential and the way they have been utilized and managed. But most have one thing in common—they show marked advances in the development of woody vegetation. Much of this change in recent years has been detrimental to mule deer populations, particularly on lands where heavy growth of trees has resulted in decline and loss of herbs and palatable shrubs. In areas where trees are not competitive, the shrub complement is dense and reaching old age, plant vigor is low, seedlings are few, and repeated insect defoliation and browsing have taken their toll.

Urban expansion onto mule deer habitat has, of course, been an increasing problem in recent years. This underscores the need to maintain productive deer ranges elsewhere.

Mule deer habitats reached optimum levels during and following a period of extreme disturbance by livestock grazing, logging, and fire. Considering the current approach to wildland management, it is unlikely that these lands will again be disturbed as extensively as they were formerly. Thus, mule deer habitats will continue to decline in both area and quality by loss to human development and successional advances. Nonetheless, there are large areas where mule deer will receive major consideration in resource management decision making. Here, there are opportunities to maintain productive habitats by management of livestock, application of prescribed fire, mechanical treatment, and cutting of trees depending on the situation.

Longhurst and others (1981) concluded that prescribed livestock grazing has more potential for improving deer habitat than any other land use practice. These researchers propose that greater efforts should be made to minimize the detrimental effects of grazing on deer habitat, and particularly to explore the possibility of using prescribed grazing to enhance forage quality. Research on utilizing prescribed grazing systems to improve deer and elk range quality on sagebrush/grass ranges has been underway in northwestern Utah over the past 25 years (Urness 1981). This effort has demonstrated the potential for manipulating livestock grazing in ways to directly improve habitat values for big game. The applicability of this research on western ranges has its limitations, however, because permits have little flexibility in adjusting grazing patterns that allow enhancement of wildlife habitat values.

Manipulation of livestock grazing alone would not be sufficient to rehabilitate deteriorated mule deer habitats. Although the historical evidence demonstrates that livestock grazing was important in improvement of post-1900 mule deer habitats, this disturbance occurred on habitats that were in early succession following past fire disturbance. Today, most mule deer habitats are in a state of advanced succession, and thus have a markedly reduced ability to respond to the manipulation of livestock grazing only. Successional advances in many regions, particularly those invaded by conifers, will require removal of trees by cutting or fire in combination or separately to return habitats to a productive condition. Priority vegetal types on mule deer ranges in the Intermountain West include mountain shrub, sagebrush/grass, pinyon/juniper, ponderosa pine, and Douglas-fir.

Over the past 40 years, experimentation and application of prescribed fire have demonstrated that, properly applied, fire can result in an improvement of mule deer habitat. Nevertheless, the art of applying prescribed fire is a major challenge in resource management. Whether or not to use fire largely depends upon the potential of the site to respond to

fire. A wide range of plant responses are possible. Important considerations are preburn plant composition, fuel type, fire severity, burn size, and postburn foraging intensity. Following fire, it may take 20 years or more to realize optimum deer habitat. Fire sets plant succession back to early seral stages that are less productive of mule deer. As succession advances, however, these habitats become prime producers of mule deer.

The case for utilizing prescribed fire is supported by a trend toward increased numbers and size of wildfires, particularly in woodlands where there has been an enormous increase in living fuels. In semi-arid regions of the Intermountain West, long-term fuel buildup is resulting in uncharacteristically severe wildfires, followed by very slow vegetal recovery. These fires are more severe than they were previously because of the marked increase in woody fuels. This undesirable trend will continue and may accelerate in the future, unless fuels are substantially reduced.

There is widespread opportunity to break up fuel continuity and produce mosaics that will not only benefit mule deer, but reduce the likelihood of extensive wildfires. In grasslands that have been invaded by conifers, there is potential for cutting living trees for firewood and other purposes followed by prescribed fire. Use of moderate-intensity prescriptions in plant communities such as sagebrush/grass, aspen, and mountain shrub (*Ceanothus* spp., Scouler's willow (*Salix scoulerana*), serviceberry, chokecherry, mountain maple, Gambel oak, etc.) would result in nutrient increases, increased palatability, and increased forage availability. Surface fires of moderate intensity, after thinning or selective cutting, have good potential for improving mule deer habitat in ponderosa pine and Douglas-fir forests. Not only does fire promote regeneration of crown-sprouting shrubs, but it also bares mineral soil that allows establishment of herbs and shrub seedlings such as bitterbrush and mountain-mahogany. Application of surface fire is also compatible for silviculture, as ponderosa pine regeneration is favored over the less valuable Douglas-fir.

The future of maintaining productive mule deer habitats in the Intermountain West lies in purposeful disturbance—not protection from perturbations. The objective in managing perturbations for improved mule deer habitat should be to achieve a mosaic of seral stages on a given deer range, rather than taking no action which results in vast expanses in mostly advanced successional stages.

The only practical and acceptable ways of perpetuating productive mule deer habitats are by management of livestock, mechanical treatment, cutting of trees, and use of prescribed fire. The appropriateness of these approaches will depend upon local vegetal conditions, administrative constraints, and public attitudes. Mule deer habitats cannot be brought back to earlier productive conditions that occurred throughout the West. There is, however, much opportunity to rejuvenate mule deer habitats in priority areas.

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APPENDIX 1: PRE-1900 REPORTS OF MULE DEER IN MONTANA, WYOMING, UTAH, IDAHO, AND NEVADA

Reference	Observer	Date	Location	Observations
Montana				
Thwaites 1959	Lewis & Clark	1805-06	Missouri River	Mule deer common up Missouri River to Gates of the Mountain. Uncommon in southwestern and west-central Montana except for some localities where they may have been common.
Phillips 1940	Ferris	September 1832	Southwestern Montana	Journal suggests local abundance on what may have been the Boulder drainage.
Lewis and Phillips 1923	Work	Winter 1832	Western and Southwestern Montana	Journal suggests scarcity of mule deer on Blackfoot, upper Clark Fork, and Beaverhead drainages.
Montana Historical Society 1902	J. Stuart	April 1863	Madison, Gallatin, and Yellowstone watersheds	Mule deer apparently uncommon west of Gallatin Valley; more common to the east.
Mullan 1855	Mullan	December 1863	Southwest Montana	Observed large bands of white-tailed and "black-tailed" deer at Lower Blacktail Deer Creek near site of Dillon, MT.
Hafen and Hafen 1961	Sawyers	1865	Southeastern Montana	Reported game including deer abounded on the Little Big Horn drainage.
Ludlow 1876	Ludlow	1875	Southwestern Montana	Reported elk and deer to be numerous in the vicinity of Bridger Pass in Bridger Mountains.
Wyoming				
Thwaites 1966b	Palmer	June 1846	Southeastern Wyoming	Mule deer were apparently plentiful on the North Fork of the Platte River.
Hafen and Hafen 1961	Rockafellow	August 1865	Central Wyoming	Observed a group of blacktailed deer while crossing the Pumpkin Buttes.

Doane 1877	Doane	December 1876	West-central Wyoming	No deer seen on trip down Snake River between Jackson and Alpine.
Endlich 1879	Endlich	1877	Southwest and south-central Wyoming	Reported mule deer to be plentiful on west slope of Wind River Range and quite abundant in some localities along the Sweetwater and Seminole Hills.
Lott 1940	Wise	September 1880	North-central Wyoming	Killed several nice bucks on east slope of Big Horn Mountains.
Idaho				
Spaulding 1956	Ross	November 1823	Central Idaho	Deer numerous on Salmon River below Stanley.
Rich 1950	Ggden	June 1826	Southwest Idaho	Deer scarce year long between Wood River, ID, and Burnt River in eastern Oregon.
Lewis and Phillips 1923	Work	April 1832	East-central Idaho	Journal suggests deer scarcity on Salmon River between mouth of Pahsimori River and present-day Challis, ID.
Lewis and Phillips 1923	Work	June 1832	Southwest Idaho	On middle fork of Payette River party was forced to kill horses for food. Old tracks indicated that deer were numerous earlier.
Thwaites 1966a	Townsend	July 1833	Southeast Idaho	Game scarce in Soda Springs locality.
Thwaites 1966a	Townsend	August 1833	South-central Idaho	Mule deer numerous on upper Lost River.
F. Wislizenus 1912	Wislizenus	July 1839	Southeast Idaho	Soda Springs locality did not abound in game. Game scarce in Blackfoot Mountains.
Phillips 1957	G. Stuart	1858	Southeast Idaho	Game scarce between Fort Hall and Fort Bridger.
Thompson and Thompson 1982	Leigh	1876	Southeast Idaho	Deer uncommon in Snake River drainage east of present-day Idaho Falls.
Utah				
Anonymous 1946	Escalante	1776	Utah	Party killed buffalo, traded with Indians for bighorn sheep meat, but no mention of deer in what is now Utah.

APPENDIX 1. (Con.)

Reference	Observer	Date	Location	Observations
Anonymous 1946	Smith Ferris Walker Russell	1826-27 1830-34 1833-34 1834-40	Northern Utah Northern Utah Northern Utah Northern Utah	These trappers described the occurrence of buffalo, antelope, elk, and incidental deer. Utah area generally did not have abundant game. Indians depended mainly on insects, seeds, fruits, and small animals as sources of food.
W. Egan 1917	H. Egan	1847	Northern Utah	Reported game to be scarce on west slope of the Wasatch Mountains.
Stansbury 1852	Stansbury	1847-48	Northern Utah	Came very scarce in Salt Lake valley during winter of 1847-48.
Rich 1950	Ogden	May 1826	Nevada Northeastern Nevada	Hunters in quest of deer in upper Bruneau River watershed returned without success. No tracks were seen.
Williams 1971	Ogden	December 1828	Northeast Nevada	No deer observed during 8-day trip east which included crossing of Toana and Pequop Mountain's deer winter ranges.
Williams 1971	Ogden	April-June 1829	Northeast and north-central Nevada	Return trip. No deer were seen despite numerous hunting excursions by most experienced hunters. Country covered included parts of Independence, Bull Run, and Santa Rosa Ranges.
Haines 1971	Work	May-June 1831	Northeast Nevada	No deer seen from May 24 to June 27 between what is now Deeth and McDermitt, NV. Route of travel included Marys River, Charleston, Wildhorse Reservoir, Independence Valley, Humboldt River, and west side of Santa Rosa Range.
Fremont 1887	Fremont	January 1844	Western Nevada	Tracks in one locality suggests deer may have been numerous in some areas along the east slope of the Sierra Nevada during periods of winter concentrations.
Simpson 1876	Simpson	1859	Eastern and central Nevada	No deer were seen during a round-trip wagon road survey between Camp Floyd, UT, and Genoa, NV.

APPENDIX 2: HISTORICAL ACCOUNTS OF VEGETAL CONDITIONS ON PLAINS AND BROAD SEMIARID VALLEYS

Reference	Observer	Date	Location	Observations
Montana				
Raynolds 1868	Raynolds	July 1859	Powder River	"Our route lay now down the valley of Powder River, which was covered with large sage bushes"
				"The grass on the river surpassed our expectations in its quality"
				"The eye grows weary of the constant sight of barren hills and blue sage."
Raynolds 1868	Raynolds	August 1859	Lower Rosebud Creek	"The entire river bottom is covered with sage"
Raynolds 1868	Raynolds	August 1859	Lower Bighorn River	"Artemisia covered the ground over which we traveled to-day, seriously inconveniencing the progress of our vehicles."
Raynolds 1868	Raynolds	August 1859	Hardin, Montana	". . . we found fine grass, the best seen this season, but it does not extend over one-fourth of a mile from the river, the balance of the valley being clay covered with the interminable artemisia."
Ludlow 1876	Ludlow	August 8, 1875	16 Mile Creek (S. of Smith Valley)	". . . the road beyond lay over a dry, yellow, gently undulating prairie, which . . . became an interminable waste of sagebrush."
Ludlow 1876	Ludlow	September 1875	Big and Little Timber Creeks, Yellowstone R.	"The country between these two streams is very poor, almost no grazing; sagebrush being the main production."
Wyoming				
Thwaites 1966b	Palmer	July 1845	North Fork Platte River to Green River	Described vegetation as predominantly sagebrush. Hills and moist areas were grassy.

(con.)

APPENDIX 2. (Con.)

Reference	Observer	Date	Location	Observations
Raynolds 1868	Raynolds	October 1859	South of Sheridan	"Following up the valley of Powder River we found our progress impeded by high sage and deep ravines"
Raynolds 1868	Raynolds	October 1859	Upper Powder River	". . . a very thin growth of bunchgrass upon some of the ridges, and the never-failing sage (<u>Artemisia</u>) completes the vegetation."
Raynolds 1868	Raynolds	May 1860	North of Rattlesnake Hills	"The country passed over was a gently rolling plateau, with no obstructions save the sage, which embarrassed the heavy wagons of the escort."
Endlich 1879	Endlich	August 1877	Jeffery City locality, Sweetwater River	"Emerging from this narrow place we see before us a wide, meadow-like flat, covered with excellent grass."
Endlich 1879	Endlich	August 1877	West of Rawlins	"The country here is very barren, being covered with sagebrush and prickly pears."
Endlich 1879	Endlich	September 1877	Crook's Gap near Green Mountains	"A long ride through sagebrush, over a sterile country, brought us to this pass."
Endlich 1879	Endlich		Sweetwater region vegetative summary	"Reaching the bluff country, we find sagebrush (<u>Artemisia tridentata</u>) very prevalent. Its appearance usually indicates a dry, sandy region."
				"All the low country lying east of the Wind River Mountains and north of the Sweetwater Plateau contains sagebrush and cactus (<u>Opuntia</u>)."
				"On the Sweetwater Plateau but very little timber occurs, excepting on its north slope. There pines and quaking asp are found in the gulches, while sage covers the intervening ridges. On the southern slope of the plateau bunchgrass (<u>Eriocoma cuspidata</u>) is abundant, affording good feed for the animals."

Idaho

Rollins 1935	Stuart	September 1812	American Falls	"The country paused [passed] since yesterday morning has improved greatly--the sage and its detested relations gradually decreased, and the soil though parched, produces fodder in abundance . . ."
Haines 1971	Work	December 1830	Snake River Plains S. of Atomic City	" . . the country still maintains the same appearance except one portion of the plain which we passed which is clear of wormwood [sagebrush] and has some coarse grass peeping above the snow."
Haines 1971	Work	February 7, 1831	Below outlet of Portneuf R.	" . . was deterred from doing so by being told that the grass had been burnt in the fall by the Indians."
L. McKinstry 1975	B. McKinstry	July 1852	Snake River Plains	"Beyond Snake River the whole country is an elevated sage plain."
L. McKinstry 1975	B. McKinstry	August 1852	South of City of Rocks	" . . by an easy ascent reached a summit and as gradually descended to a valley of sage and sand . . ."
Mullan 1855	Mullan	December 1852	Snake River Plains	"Our trail crossing the Medicine Lodge Creek led through an immense sage prairie, extending about twenty miles to the north, to the Snake River on the south, and to the Tetons in the east."
Bradley 1873	Bradley	July 1872	Snake River Plains	" . . we see the rough, almost impassible, basalt-plain, thickly overgrown with sagebrush, stretching away toward Market Lake [Mud Lake]."
Bradley 1873	Bradley	July 1872	Upper Snake River Plains-Rexburg locality	"The low plain bordering Henry's Fork on the west is from two to eight or ten miles in width, partly well grassed, though with many dense patches of sagebrush."
Bradley 1873	Bradley	July 1872	Upper Snake River Plains-NE of St. Anthony	"The abundant growth of grasses, sedges, and other flowering herbs shows plainly that only slight irrigation would be necessary to make this valuable farming-land . . ."

Utah

Cottam 1947	Father Escalante	1776	Utah Lake	Father Escalante speaks of grass on plains having burned. Cottam concludes that grass, sufficient to carry prairie fire, must have been fairly abundant.
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(con.)

APPENDIX 2. (Con.)

Reference	Observer	Date	Location	Observations
Stewart 1941	J. Mathews J. Brown	July 1847	Salt Lake Valley	Crossed valley to westside and reported that the wild sage is very plentiful--showing the land is not as rich as along the Wasatch front.
Christensen and Johnson 1964	Farrer	October 1849	Round and Pavaunt Valleys	" . . . we came into a large wide Canion feed growing very luxuriantly. We came into an extensive valley little water sage Brush plentiful feed pretty good"
Christensen and Johnson 1964	Smith	December 1850	Round Valley	" . . . crossed another wider creek a little timber growing on it. traveled thro a good deal of Sage"
Christensen and Johnson 1964	Beckwith	October 1853	NW of Holden	"Camped in a beautiful valley. Snow 12 inches deep. Good feed, bunchgrass, plenty sage brush"
Simpson 1876	Simpson	May 1859	Steptoe Valley	" . . . this whole valley, some fifty or sixty miles in diameter, is one vast artemisia plain surrounded by grassy mountains."
Simpson 1876	Simpson	May 1859	Huntington Valley	"This is a poor, arid valley, perfectly useless for cultivation where we cross it further, south there is a great deal of good, available pastoral and cultivatable soil."
Simpson 1876	Simpson	May 1859	Valley north of Roberts Creek	"As usual the artemisia covers the valley and in this locality is quite rank in growth."
Simpson 1876	Simpson	May 1859	Big Smoky Valley	"Soils argillaceous and covered with sage and greasewood."
Simpson 1876	Simpson	May 1859	Big Smoky Valley	"Soil areno-agrillaceous, and is very thinly covered with artemisia."

Nevada

Simpson 1876	Simpson	May 1859	Reese River Valley	"The grass along it [Reese River] is luxuriant, but in many places alkaline. It is best and very abundant farther up the stream, and extends as far as the eye can reach . . . Soil argillo arenaceous and covered with wildsage and greasewood."
Beckwith 1855	Beckwith	1855	Humboldt River	"The valley of the Humboldt is more or less covered with the several varieties of artemisia, which occupy so large a proportion--at least nine-tenths of the plains--of our territory between the Rocky and Sierra Nevada Mountains, and characterize its vegetation."

APPENDIX 3: HISTORICAL ACCOUNTS OF VEGETAL CONDITIONS ON MOUNTAIN VALLEYS AND SLOPES

Reference	Observer	Date	Location	Observations
Montana				
Haines 1965	Russell	September 1835	Ruby Range	"Traveled about 18 miles over high rolling hills beautifully clothed with bunchgrass."
Mullan 1855	Mullan	December 1853	Bitterroot Valley	"The soil of this portion of the valley is principally of a rich dark-colored loam . . . the whole being covered with a growth of rich and luxuriant grass."
Mullan 1855	Mullan	December 1853	Horse Prairie, Red Butte	"Our course during the earlier part of this day . . . lay over a series of low sandy ridges, covered with the artemisia, growing from three to four feet high."
Mullan 1855	Mullan	December 1853	Red Rock Creek	"We found the soil of this valley principally of a yellowish or grayish yellow colored clay, upon which through-out its whole length, the wild sage grows in the greatest abundance. On the lower and the upper portions of this valley we found the grass to be exceedingly rich, but near the middle nothing growing save the wild sage bushes."
Mullan 1855	Mullan	December 1953	Melrose Valley	"The grass of the valley we found to be very good. The soil, however, is poor, being principally a yellowish clay, that bakes in the sun."
Phillips 1957	Stuart	October 1857	Monida Pass	"Instead of the gray sagebrush covered plains of Snake River, we saw smooth rounded hills and sloping bench land covered with yellow bunchgrass that waved in the wind like a field of grain."
Raynolds 1868	Raynolds	September 1859	Southeast Montana	Reported extensive grasslands in the upper watersheds of the Little Big Horn, Rosebud, and Tongue Rivers.
Raynolds 1868	Raynolds	July 1860	Little Belt Mountains and Smith Valley	"The grass through which we have passed to-day has been unequalled in luxuriance and richness, surpassing the fertile meadows of eastern farms."

Hayden 1873	Hayden	1872	Horse Prairie	"... the soil is fertile, and during the summer season the grass is excellent . . ."
Hayden 1873	Bradley	1872	Upper Madison River	"... the volcanic sand being only sparsely covered with a growth of coarse plants, often including much sagebrush."
Hayden 1872	Hayden	1871	Raynold's Pass	"The Low or Raynold's Pass is like a lawn--smooth and covered with grass . . ."
Hayden 1872	Hayden	1871	Upper Madison River	"... on both the east and west branches, which enter the Madison near together at this point, the surface is covered with a luxuriant growth of grass The slopes from the base of the mountains on either side down to the river are most admirable illustrations of lawns on a grand scale."
Ludlow 1876	Ludlow	August 8, 1875	Bridger Pass Bridger Mountains	"Grass is abundant, even among the timber . . ."
Thwaites 1966b	Palmer	1845	Cokeville region	"The hills bordering on Bear River on this days travel are very high and rugged; they are covered with grass."
Raynolds 1868	Raynolds	June 8, 1860	Upper Gros Ventre River	"... grass has become abundant, while flowers surround use on every side."
Montana Historical Society 1902	DeLacy	August 25, 1863	Jackson Hole (lower Antelope Flats)	"It is covered with fine grass; the soil is deep in many places . . ."
			(upper Antelope Flats)	"In the evening we took a northwest course toward the river, passing over a plain, part of which was covered by the largest and thickest sage-brush that I had ever seen."
Montana Historical Society 1902	Stuart	May 26, 1863	Wind and Popo Agie Rivers	"Plenty of cottonwood along the river, and gravelly, greasewood, and sagebrush plains . . . Abundance of bunch-grass in the hills, but very little of any kind along the river."

(con.)

APPENDIX 3. (Con.)

Reference	Observer	Date	Location	Observations
Jones 1875	Jones	June 27, 1873	East slope of Wind River Mountains	"The long slopes of the foothills of the mountains are here covered with a splendid growth of grass"
				"The country is rolling, with a good soil, supporting a fine growth of grass, but no trees."
Jones 1875	Jones	July 17, 1873	Middle Fork Owl Creek trib. to Bighorn River	"The mountain-slopes are generally rounded, and covered with a fine growth of grass. . . ."
Jones 1875	Jones	July 21, 1873	Cottonwood Creek	"The line of march lay through the grassy and well watered foothills of the mountains."
Jones 1875	Jones	July 22, 1873	Gooseberry Creek	"The country is still high-rolling, with fine grass all over it, and a few trees."
Endlich 1879	Endlich	1877	Sweetwater Plateau	"On the southern slope of the plateau bunchgrass (<u>Eriocoma cuspidata</u>) is abundant"
Idaho				
Fremont 1887	Fremont	1843	Malad Summit	"In the afternoon we entered a long ravine leading to a pass in the dividing ridge between the waters of Bear River and the Snake River . . . our way being very much impeded, and almost entirely blocked up, by compact fields of luxuriant artemisia."
				"All the mountain sides here are covered with a valuable nutritious grass, called bunchgrass"
Thwaites 1966b	Palmer	1845	Mountain Home locality	". . . we directed our course up a stony hill; thence over a sage plain to a spring branch . . . in general, the mountains here are covered with grass"
Stansbury 1852	Stansbury	September 22, 1849	Lava Hot Springs locality	"From the top of the bluff, an extensive level plain, clothed with grass, is spread out before us like a beautiful picture"

Raynolds 1868	Raynolds	June 25, 1860	Henry's Lake	"The prairie was beautiful with its luxuriant growth of young grass, and bands of antelope were scattered about us on all sides."
Hayden 1872	Hayden	1871	Henry's Lake	"Henry's Lake was at our feet To the west there is a beautiful grassy valley"
				"Far southward extends the valley of Henry's Fork The upper portion, for an extent of twenty to twenty-five miles in length and five to ten miles in breadth, is like a meadow, covered with a luxuriant growth of grass"
Bradley 1873	Bradley	1872	Teton Basin	"Most of the plain is thickly covered with a luxuriant growth of grasses and other good forage plants, though some small areas are sandy and comparatively barren."
Hayden 1873	Hayden	1872	Pocatello	"Fort Hall is a small but exceedingly neat post . . . and is located in a beautiful fertile grassy valley, among the foothills on the east side of the Snake River Basin"
Hayden 1873	Hayden	June 1872	Pleasant Valley	". . . as we approach Pleasant Valley the hills are covered with a drift deposit These hills are covered over with grass."
Hayden 1873	Hayden	June 1872	Monida Pass region	"On the morning of June 29, we left the beautiful valley behind us and traveled 9 miles north . . . for ten or fifteen miles, the rounded, grass covered hills prevailed"
Thomas 1873	Thomas	1872	Blackfoot-Shelley region	". . . gazing from the summit of this ridge on the endless succession of the smooth, grassy ridges"
Thompson and Thompson 1982	Leigh	August 24, 1876	Rexburg-Canyon Creek region	"Reached Canyon Creek at 11 o'clock after a 15 mile ride over flat rolling country covered with excellent grass and free of sage."
St. John 1879	St. John	1877	Taylor Mountain	"The wolverine opens out into a beautiful little mountain basin . . . on the north undulating grass-covered slopes interspersed with groves of aspen"

(con.)

APPENDIX 3. (Con.)

Reference	Observer	Date	Location	Observations
St. John 1879	St. John	1877	Antelope Flat- SE of Ririe	"... northward it is continued in a lower and narrower ridge, which finally expands into a plateau overlooking the grassy upland on the borders of the Snake plain."
Hull and Hull 1974	Ferris	1832	Cache Valley	"One of the most extensive and beautiful valleys of the Rocky Mountain Range . . . , producing everywhere most excellent grass"
Fremont 1887	Fremont	1843	Spanish Fork	"The streams are prettily and variously wooded, and everywhere the mountain shows grass and timber."
Fremont 1887	Fremont	1844	Mountain Meadows	"We found here an extensive Mountain Meadow, rich in bunch-grass and fresh with numerous springs The meadow was about a mile wide, and some ten miles long, bordered by grassy hills and mountains."
Cottam 1947	Bryant	July 30, 1846	Davis County to Beck's Hot Springs	Described the slopes as grassy along the Wasatch Front.
Cottam 1947	Gunnison	1849	Salt Lake Valley	"The valleys afford perennial pasturage, but the hillsides furnish bunchgrass only during the warm months of the year."
Cottam 1947	Stansbury	November 1849	Tooele Valley	"The grass is very abundant and numerous springs are found on both sides of [the valley]."
Cottam 1947	DeLaMare	1850's 1860's	Tooele Valley	On arriving as a boy, Mr. DeLaMare remembered a valley full of high waving grass.
Cottam 1947	Pratt	April 14, 1857	Mountain Meadows	"Some thousand or fifteen hundred acres of bottom or meadow lands were spread out before us like a green carpet richly clothed with a variety of grasses The surrounding hills are abrupt . . . and everywhere richly clothed with the choicest kind of bunchgrass"

Nevada

Kern 1876	Kern	1845	Secret Pass	"The stream, after winding among the grass-covered hills, emerges into a plain . . ."
Kern 1876	Kern	1845	Emigrant Pass	"Ascending some grassy hills, encamped at several springs. Bunch-grass plenty . . ."
Utah Historical Society 1932	Bigler	1848	Wells	"The surrounding country looks beautiful with low mountains all around with plenty of grass."
Simpson 1876	Simpson	May 1859	Egan Mountains	". . . on the mountain-sides and in the ravines is to be found a great deal of grass."
Simpson 1876	Simpson	May 1859	Diamond Mountains	". . . we reached the mouth of Egan Canon, down which a fine, rapidstream runs, and on which we camped. Grass on the side of the mountain."
Simpson 1876	Simpson	May 1859	North end Monitor Range	"Grass along the stream, and plenty higher up on slopes of the mountains."
Simpson 1876	Simpson	May 1859	Simpson Park Range	"In 4.3 miles, cross Saw-wid Creek, a rapid stream . . . Fine grass on it toward the mountains."
Simpson 1876	Simpson	May 1859	Simpson Park Range	". . . in the canyons higher up in the mountains, is plenty of grass."
Simpson 1876	Simpson	May 1859	Willow Creek-Simpson Park Range	"The mountain-range immediately to our west is called by the Indians the Pah-re-ah or Water Mountain, on account of the many streams which flow down its sides into Kobah Valley, and on them is to be seen an abundance of grass."
Simpson 1876	Simpson	May 1859	Reese River Valley	"There is a great deal of meadow along it and bunchgrass on the sides of the mountains . . ."
Simpson 1876	Simpson	May 1859	Toiyabe Mountains	"The grass along it is luxuriant, but in many places alkaline. It is best and very abundant farther up the stream, and extends as far as the eye can reach."
Simpson 1876	Simpson	July 1859	Toiyabe Mountains	"The grass in Reese Valley, through the canons we have passed to-day, as well as everywhere nearly on the mountains, very abundant; more so than when we passed before."

Gruell, George E. Post-1900 mule deer irruptions in the Intermountain West: principal cause and influences. General Technical Report INT-206. Ogden, UT. U.S. Department of Agriculture, Forest Service, Intermountain Research Station; 1986. 37 p.

Tests hypotheses for mule deer population increases between the early 1930's and mid-1960's. Concludes that livestock grazing and absence of fire converted vast areas of grasses and forbs to woody plants favored by mule deer. Mule deer populations, therefore, irrupted between 1930 and 1965 and have since experienced a decline as plant succession moves toward shrub senescence and trees. Habitat management alternatives are discussed.

KEYWORDS: mule deer, livestock, fire, grass, shrubs

INTERMOUNTAIN RESEARCH STATION

The Intermountain Research Station provides scientific knowledge and technology to improve management, protection, and use of the forests and rangelands of the Intermountain West. Research is designed to meet the needs of National Forest managers, Federal and State agencies, industry, academic institutions, public and private organizations, and individuals. Results of research are made available through publications, symposia, workshops, training sessions, and personal contacts.

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